Reference: *Biol. Bull.*, 144: 132–150. (February, 1973)

PACHYCHELES MONILIFER (DANA, 1852): THE DEVELOPMENT IN THE LABORATORY OF LARVAE FROM AN ATLANTIC SPECIMEN WITH A DISCUSSION OF SOME LARVAL CHARACTERS IN THE GENUS (CRUSTACEA: DECAPODA; ANOMURA

ROBERT H. GORE

Smithsonian Institution, Ft. Pierce, Florida 33450

The porcellanid crab genus *Pachycheles* which is essentially tropical and worldwide in distribution consists of 14 Atlantic, 18 Eastern Pacific and 11 Indo-Pacific species (see Haig, 1956; 1960; 1966b). The larval development is known completely or in part for only six species (Table I), two from each of the mentioned oceans. In the western hemisphere two species of the genus are known to occur on both sides of the Panamanian isthmus, *Pachycheles chacei* Haig, 1956 and *P. monilifer* (Dana, 1852, 1855). The eastern Pacific record of the latter species, however, is based on a single juvenile female collected at La Libertad, Ecuador. Thus, it may not be *P. monilifer* but a new, although very closely related, species (see Haig, 1960, page 162). In the Atlantic *P. monilifer* is known to occur from Sebastian Inlet, Florida (a northern extension of range hereby noted in this study) to Ilha da Victoria, Brazil (Haig, 1966a).

Previous studies on larvae from other trans-Panamanian porcellanid crabs have shown that Atlantic larvae differ from their eastern Pacific counterparts in many respects (Gore, 1970, 1971, 1972a). Hence, the larval development of *Pachycheles monilifer* is of interest for additional reasons besides that of of identifying such larvae in the plankton. If *P. monilifer* does indeed have an eastern Pacific population then it is of interest to compare the larvae of the Atlantic population with that of the eastern Pacific to determine what differences, if any, exist between the two. Secondly, should the Pacific specimen recorded by Haig (1960, page 160) ultimately prove to belong to a specifically distinct population then comparison may still be made between the larvae of both species as a possible means of providing further grounds for their separation (see *e.g.*, Gore and Abele, in press). In addition, continued studies on larvae reared from known adults may allow elucidation of relationships in the genus as well as providing identification of such larvae on a worldwide basis.

In this paper the complete larval development of an Atlantic specimen of *Pachycheles monilifer* is described and illustrated. The larvae are compared with those known from other species in the genus and some tentative features which may characterize the genus on a worldwide basis are suggested.

Materials and Methods

Two ovigerous females were collected from the Indian River region of the central Florida east coast. One was taken at Rio Mar Reef, Vero Beach, the other

at Sebastian Inlet, on April 12 and 13, 1972, respectively. Both inhabited the interstices of phragmatopomid worm reefs common in the areas. Each female occurred with a male. Prior to this report *Pachycheles monilifer* was known only as far north as Hillsboro Reef, in south Florida (Haig, 1956, page 14).

The females were returned to the Harbor Branch Foundation Laboratory, Ft. Pierce, Florida (HBFL) placed in 19 cm diameter glass bowls filled with non-flowing seawater (34‰) until hatching occurred on 13 April. A series of 48 zoeae were placed, one each, in individual compartments of 24-compartmented rearing trays. No controlled temperature units were used. Instead, all stages were exposed to ambient light, and were held at room temperature which was adjusted via central reverse-cycle air conditioning to maintain a water temperature of about 28° C (± 2 C°, mean = 27.8° C). Water was changed and *Artemia* nauplii were provided as food every day. Salinity of ocean water stored in a 13-gallon container and used throughout the study was 34‰. Measurements of zoeae and megalopae were made with a Wild slide micrometer and are expressed as the arithmetic average of the specimens examined. For further details involving rearing, measuring and describing of larvae consult previous studies by Gore (*e.g.*, 1970, 1972a).

A spent female and a complete series of larval stages are deposited in the National Museum of Natural History, USNM 141323, 141324; a second series will be deposited in the British Museum of Natural History.

Results

Rearing experiment

Pachycheles monilifer hatches as a pre-zoea, remaining thus for as little as five minutes or up to one hour before molting to the first zoeal stage. This stage is not described.

At temperatures of 26.5–28.5° C the first zoeal stage lasts four to six days, but usually five days before molting to stage II. At temperatures of 28.5 to 30° C the second zoeal stages lasts five, usually six, and rarely as long as nine days. At temperatures of 26.5–28.5° C the megalopal stage lasts from six to 10 days, with

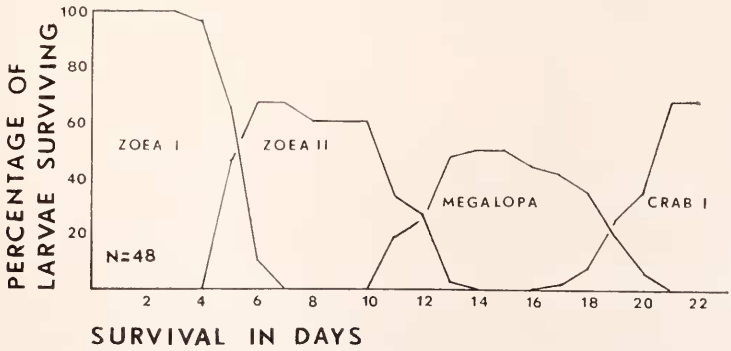

Figure 1. Percentage and duration of survival at room temperature of larvae of *Pachycheles monilifer* (Dana). N reflects the number of larvae reared in the series.

TABLE I

Comparison of some zoeal features in six species of Pachycheles*

ZOEA I	*P. monilifer*	*P. haigae*	*P. pubescens*	*P. rudis*	*P. stevensii*	*P. natalensis*
Antenna						
Exo::Endo	1.5×	2×	1.75-2×	2×	*ca.* 2×	¼×
Exopod	3 spines	4 spines	3-4 spines	3 spines	3 spines	3 spines
Mandible						
Palp	Absent	Absent	Absent	Absent	Absent	Absent
Maxillule						
Endopod	4 setae	4 setae	3-4 setae	4 setae	4 setae	4 setae
Endites	9 basal 8 coxal	9 basal 8 coxal	8-9 **basal 8*-9 coxal	9 basal 8-9 coxal	7 basal** 8 coxal**	9 basal** 8 coxal**
Maxilla						
Endopod	4,2,3 setae	9(?4,2,3)**	3-4,2,3 setae	4,2,3 setae	4,2,3 setae	9(?4,2,3)**
Scaphognth.	4-5 + 1 setae	7 + 1 setae	6-7 + 1 setae	6-7 + 1 setae	6 + 1 setae	7 + 1 setae
Maxilliped 1						
Coxopod	2 setae	No data	2 setae	2 setae	No data	No data
Basipod	2,2,2,3	2,2,3,3	2,2,2-3,3	2,2,2,3	?,2,2,3**	2,2,3,3
Endopod	3,3,2+3,8-9+1	2,4,3+4,10+1	2-3,3,1-2+3, 8-9+1	3,2,2+3-4,7-9+1	3,3,2+3,6+1**	"2,4,6,8" = 2,4, 2+4,8+1?**
Maxilliped 2						
Coxopod	Naked	No data	Naked	Naked	No data	No data
Basipod	1,2	1,1	1,2	1,2	1,2†	1,2
Endopod	2,2,1+2,5+1	3,3,1+1,7+1	2,2,1+2,5-6+1	2,2,1+2,5+1	2,2,1+2,4+1†	2,2,1+2,5+1
Abdomen somites						
Lateral spines	3,4,5	5	4,5	4,5	3**,4**,5	5
Dorsal teeth	Present	No data	Present	No data	Present	No data
Telson setae						
Distal Hooks	1,2	1,2	1,2	1,2	1,2	1,2,3,4,5
Carapace margin	Serrate	Smooth**	Smooth**	Smooth**	Serrate	Smooth**
ZOEA II						
Antennule						
Aesthetascs	4,5,3,3,2+3-4	"8"+"a series"	4,5,3,3,2+3-4††	4,5,3,3,2+3-4	No data	No second stage
Protopod	No long seta	No long seta	1 long seta	1 long seta	No data	data available

TABLE I—(*Continued*)

ZOEA II	*P. monilifer*	*P. haigae*	*P. pubescens*	*P. rudis*	*P. stevensii*	*P. natalensis*
Antenna						
Exo::Endo.	$\frac{2}{3}$	$\frac{2}{3}$**	$\frac{2}{3}$	$\frac{2}{3}$–$\frac{3}{4}$	$\frac{1}{2}$	
Exopod	3 hairs	Naked	Naked	Rudimentary spines or naked	Naked**	
Mandible						
Palp	Present	Absent	Present	Present	Present	
Maxillule						
Endopod	4 setae	4 setae	4 setae	4 setae	4 setae†	
Endites	10 basal	11–12 basal	10 basal	10 basal	No data	
	10 coxal	10 coxal	10–11 coxal	10–11 coxal	No data	
Maxilla						
Endopod	4,2,3 setae	6,2 setae	4,2,3 setae	4,2,3 setae	No data	
Scaphognth.	25 setae	24 setae	21–22 setae	20–22 setae	No data	
Maxilliped 1						
Coxopod	2 setae	No data	2 setae	2 setae	No data	
Basipod	2,2,2,3	2,2,3,3	2,2,2,3	2,2,2–3,3	?,2,2,3**	
Endopod	3+1,3+1,2+3+1, 9–10+1	2+1,4+1,3+4 +1,10+1**	3+1,3+1,1+3+1 6–10+1	3,2+1,1–2+3–4 +1,8–9+1	3+1,3+1,2+3+1, 7–8+1**	
Maxilliped 2						
Basipod	1–2,2	1,2**	1,2	1,2	1,2**	
Endopod	2+1,2+1,1+2+1, 5+1	3+1,3+1, 1+2+1,7+1	2+1,2+1,1+2+1 5–6+1	2–3,2+1,1+2+1, 5+1	2+1,2+1,1+2+1, 4(?5)+1	
Maxilliped 3	2 setae	2 setae	4–6 setae	2 setae	1–3 setae	
Telson setae						
Distal Hooks	1,2	1,2	1,2	1,2	1,2	
Carapace margin	Serrate postero-laterally	Smooth**	Smooth**	Smooth**	No data	

* Species data from authors as follows: *P. haigae*, Boschi, Scelzo and Goldstein, 1967; *P. pubescens*, Gonor, 1970, MacMillan, 1972; *P. rudis*, Gonor, 1970, Knight, 1966; *P. stevensii*, Kurata, 1964; *P. natalensis*, Sankolli, 1967.

** No specific description, data interpreted from illustration.

† Probable situation based on stage II illustration.

†† Most commonly occurring situation.

most molting to crab 1 around day seven or eight. The temperatures just cited reflect those prevailing during the stages discussed. The duration of these stages and the percentage of larval survival throughout the study is expressed in Figure 1.

Sea water temperatures monitored in the Indian River adjacent to HBFL were generally 1–2.5° C lower than laboratory temperatures. For this reason the duration of larval development in the laboratory is considered to be close, although perhaps not identical, to that which occurs in nature at this time of year. If anything, because of slightly higher temperatures, the laboratory-reared specimens might have attained each developmental stage slightly faster than their counterparts in the plankton, although there is no way to determine if this was so. At any rate, *Pachycheles monilifer* is capable of completing its larval development under laboratory conditions in as little as 15 days, although the usual time is close to three weeks according to data obtained from this study.

Description of the Larvae

Zoea I

Carapace length: 1.47 mm
Number of specimens examined: 10

Carapace: (Fig. 2, A). Typically porcellanid, with elongate rostral and posterior carapace spines; former heavily armed overall with spinules to its tip and up to six times carapace length (CL); latter from 2.6–3.0 × CL. Lower margin of carapace from just posterior of eye to origin of posterior spine distinctly armed with numerous small spinules, becoming large recurved spines along ventral margin of posterior carapace spines; remainder of posterior spines covered with small nubs dorsally, and to a lesser extent, on interior margin. Three pair of setae dorsally on carapace, two pair anterior to eyes, third pair above midgut. Eyes sessile.

Antennule: (Fig. 3, A). An elongate slightly swollen rod; three aesthetascs, three setae, as shown.

Antenna: (Fig. 3, B). Endopodite fused to protopodite, a single thin hair at tip next to small, distinct spine; exopodite half again as long as endopodite, three distinct curved spines along upper margin, as shown.

Mandibles: (Fig. 3, C). Asymmetrical, heavily dentate processes; left with about 10 small teeth in semi-circle when viewed from interior; right with large molar process.

Maxillule: (Fig. 3, D). Endopodite unsegmented, four terminal setae, basal and coxal endites with 6, 3, and 5, 3, spines and setae, respectively.

Maxilla: (Fig. 3, E). Endopodite unsegmented, setae progressing terminally 4, 2, 3; lobes of basal endite, distally and proximally, with 3, 5, and 3, 4, spines and setae, respectively; those of coxal endite 2, 1, and 4, 3; scaphognathite with four (occasionally five) setae around outer margin, plus one long apical seta.

Maxilliped 1: (Fig. 3, F). Coxopodite with two setae posteriorly; basipodite setate progressing distally 2, 2, 2, 3 (occasionally 2, 3, 2, 3); endopodite setae 3, 3, 2 + 3, 8 (rarely 9) ventrally plus one (= I) plumose seta dorsally; dorsal setules on segments as shown. Exopodite indistinctly two-segmented, four natatory setae.

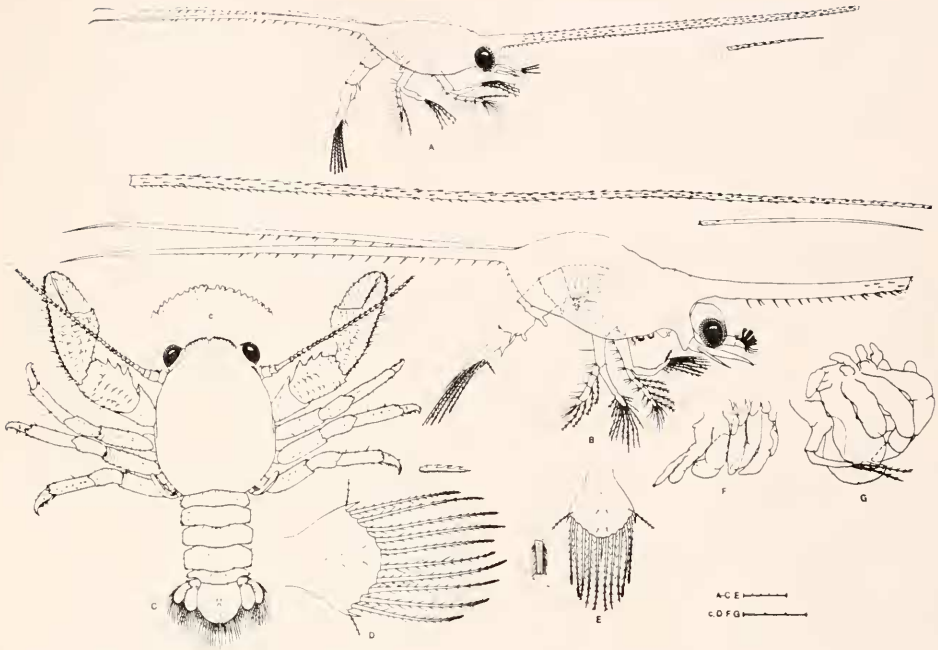

FIGURE 2. The zoeal and megalopal stages of *Pachycheles monilifer* (Dana); A, First zoea; B, Second zoea; C, Megalopa; c, Detail, megalopal frontal region; D, Telson, first zoea; E, Telson, second zoea; F, Maxilliped 3 and pereiopods, late stage first zoea; G, Same, late stage second zoea. Scale lines equal a total of 0.3 and 0.5 mm according to divisions.

Maxilliped 2: (Fig. 3, G). Coxopodite naked; basipodite setae 1, 2; endopodite setae 2, 2, 1 + 2, 5 + 1; setules dorsally on segments as shown; exopodite as above.

Maxilliped 3 and pereiopods: (Fig. 3, H). Small, amorphous buds; gill buds present in late stage; bud of future maxilliped endopodite elongate but without segmentation; no setae present during stage but may be extruded just prior to subsequent molt (Fig. 2, F).

Abdomen: (Fig. 2, A). Lateral spines present on somites 3, 4, 5, increasing in size posteriorly; dorsal posterior margin of above somites armed with series of minute teeth or spinules; pleopod buds visible only as primordia in late stage.

Telson: (Fig. 2, D). Fifth pair of plumose setae on central prominence of telson; setae 1 and 2 armed with distinct hook-like spinules at tips (detail), remaining setae appear serrate but without spines; large lateral spines of telson smooth; anal spine present.

Color: Rostrum and posterior carapace spines diffusely orange, all somites of abdomen with at least one red-orange chromatophore dorsally and ventrally, two ventrally on somites 1 and 5; when chromatophores are expanded entire abdomen

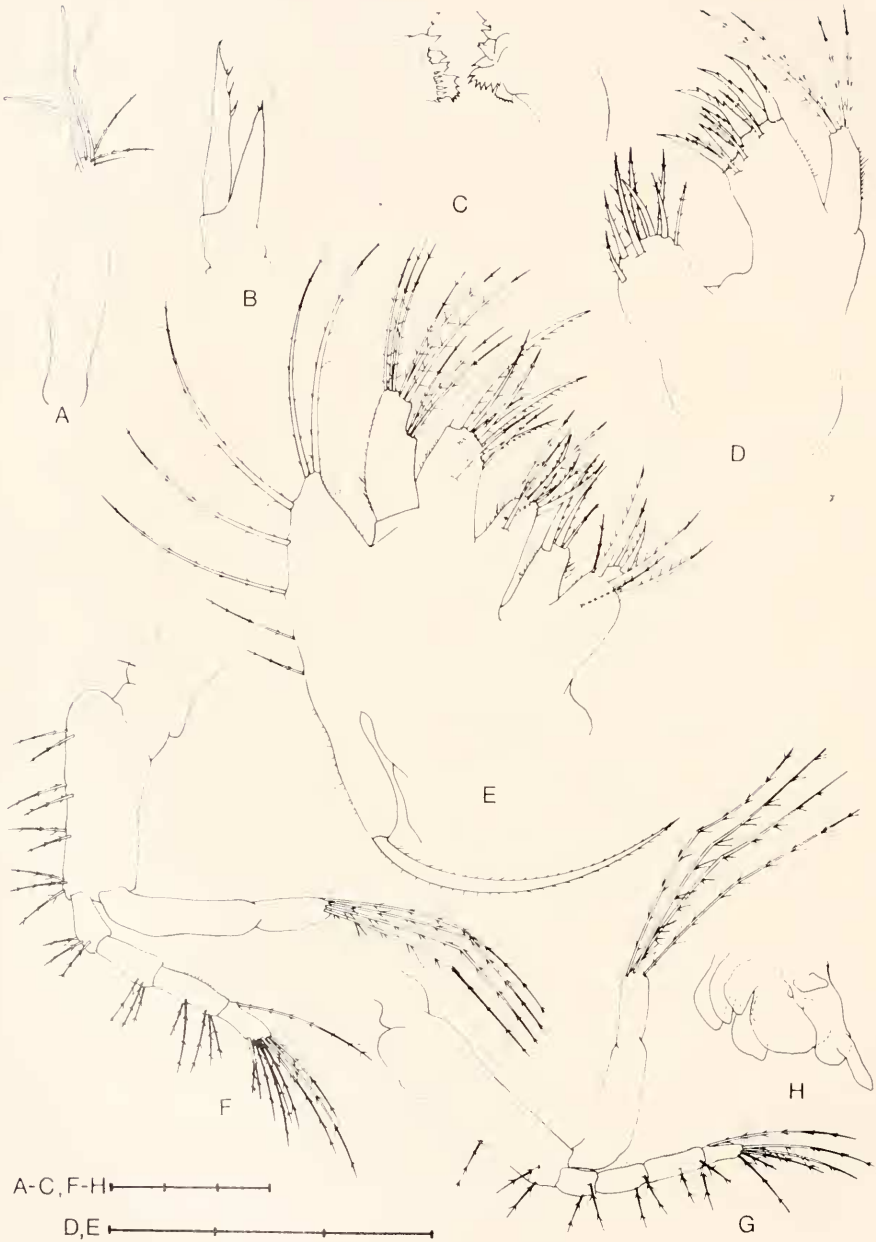

FIGURE 3. First zoeal appendages of *Pachycheles monilifer* (Dana); A, Antennule; B, Antenna; C, Mandibles; D, Maxillule; E, Maxilla; F, Maxilliped 1; G, Maxilliped 2; H, Maxilliped 3 and pereiopods, early stage. Scale lines equal 0.3 mm.

appears ringed with red-orange bands; same color extends ventrally along underside of carapace between maxillipeds and over entire mouthpart region; telson with three large orange chromatophores, two laterally toward abdomen, one mesially near central prominence; eyes dull green with black eyespots.

Zoea II

Carapace length: 2.35 mm
Number of specimens examined: 10

Carapace: (Fig. 2, B). Now more inflated; armature of rostral and posterior spines most developed ventrally, in two to four rows; rostral spine up to five times CL; posterior spines nearly twice CL; ventral margin of carapace now unarmed except for postero-lateral margin where from six to 10 small spinules appear; dorsal setae on midline of carapace not easily seen and may be absent in some specimens; eyes now mobile.

Antennule: (Fig. 4, A). Endopodite fused to protopodite, foreshortened, approximately $\frac{1}{2}$ exopodite length; latter with five rows of aesthetascs progressing distally as 4, 5, 3, 3, 2, plus three or occasionally four terminally and other setae as shown. Additional setae on protopodite as illustrated.

Antenna: (Fig. 4, B). Exopodite now without spinules distally but with three extremely fine hairs in their place, visible only under 40 × objective magnification. Exopodite approximately $\frac{2}{3}$ endopodite length; other setae as shown.

Mandibles: (Fig. 4, C). More heavily dentate than stage I, left with about seven large teeth in curved row along interior margin, right with massive molar process as illustrated; palp buds now present.

Maxillule: (Fig. 4, D). Endopodite segmented, retaining stage I setation; spines and setae on basal and coxal lobes: 7, 3, and 6, 4, respectively.

Maxilla: (Fig. 4, E). Endopodite segmented, retaining stage I setae of 4, 2, 3; spines and setae on endites as follows: basal distal, 3, 7, + 1 stub, proximal 3, 6, + 1 stub; coxal distal, 2, 3, + 1 strong seta, proximal 3, 5 encircling lobe, plus 1–2, scaphognathite with about 25 (± 2) around margin.

Maxilliped 1: (Fig. 4, F). Coxopodite and Basipodite setae unchanged; each endopodite segment with a dorsal plumose seta (I), formula of stage I retained (*viz.* 3 + I, 3 + I, 2 + 3 + I) except terminal segment which carries nine or very rarely 10 setae, plus one dorsally. Fine setules absent; exopodite distinctly two-segmented, 14 setae of type and position as illustrated.

Maxilliped 2: (Fig. 4, G). Basipodite may rarely have 2, 2, instead of 1, 2, setae ventrally; endopodite setae 2 + I, 2 + I, 1 + 2 + I, 5 + I; exopodite as above. The only variation seen on these appendages was in the third segment of maxilliped 1 in one specimen, with two long dorsal setae instead of one, and in the other setae of both maxilliped 1 and 2 noted above.

Maxilliped 3: (Fig. 2, F, G). Future endopodite bud much elongate and swollen but only faintly segmented at early stage; exopodite distinctly two-segmented with two long setae terminally, these setae first appearing during molt to stage II (Fig. 2, F).

Pereiopods: (Fig. 2, G). Now well formed but mostly unsegmented buds in early stage; segmentation and gill bud enlargement proceeds throughout stage,

FIGURE 4. Second zoeal appendages of *Pachycheles monilifer* (Dana); A, Antennule; B, Antenna; C, Mandibles; D, Maxillule; E, Maxilla; F, Maxilliped 1; G, Maxilliped 2. Scale lines equal 0.3 mm.

entire mass hanging from underneath carapace shortly before ensuing megalopal molt.

Abdomen: (Fig. 2, B). Lateral spines except for somite five reduced; small spinules on postero-dorsal margin of somites 3, 4, 5, retained. Pleopod buds present on somites 2, 3, 4, 5, enlarging as stage progresses.

Telson: (Fig. 2, E). Fifth pair of plumose setae retained on central prominence but a median spine now also present; distal tips of plumose setae 1 and 2 still with hook-like spinules. Mesially along the shaft of each plumose seta are a series of small spinules visible only under high magnification (40 × objective; see detail).

Color: As in stage I but appearing more intense due to larger size; pereiopods become tinged with blue as they develop; expanded orange-red chromatophores on abdomen cover nearly entire somite; rostrum and posterior spines nearly completely diffused with orange; because of this any color change in these spines signalling forthcoming molt is masked.

Megalopa

Carapace length × width: 1.7× 1.4 mm.
Number of specimens examined: 8

Carapace: (Fig. 2, C). Suboval, inflated, smooth, regions fairly well delimited; frontal region produced, not expanded, projecting just beyond eyes, armed on anterior margin with a series of 12 to 14 small, sharp spinules (detail) on each side, separated in middle by distinct U-shaped notch; dorsal surface with many short stiff hairs; epibranchial angle to outer orbital angle armed with about six to eight tiny spinules, outer orbital angle otherwise little developed; epimera separated but without small pieces posteriorly which characterize the genus.

Antennule: (Fig. 5, A). Peduncle three-segmented; basal segment distinctly spinous, with additional setae as illustrated. Lower ramus three-segmented with thirteen extremely long setae, seven dorso-laterally and six latero-ventrally, placed as illustrated on proximal segment. Ventral setae may be confused with three other setae which appear on ventral surface of distal segment of peduncle (Fig. 5, A detail) but former are nearly twice as long as latter. Upper ramus five or indistinctly six-segmented; aesthetascs on segments two through five usually in the following sequence of rows and numbers; 2 rows (7, 5–6, + 1 setae), 2 rows (5, 4, + 1 seta), 2 rows (2–3, + 1 seta, 3–2), 1 row (3–4), plus additional long setae at tip of ramus. Other smaller scattered setae as illustrated on both rami.

Antenna: (Fig. 5, B). Peduncle three-segmented; basal and following movable segments spinous, and with setae as illustrated. Flagellum with 25–26 segments, number differing on either flagellum in same animal; setae around distal edges of each segment as shown.

Mandibles: (Fig. 5, C). Calcified scoop-shaped processes open on interior side; each with three-segmented palp; palp with two setae basally and about 15 short spinous seta terminally.

Maxillule: (Fig. 5, D). Endopodite unsegmented, naked except for single subterminal spine; basal endite with 17 spines, 9 adjacent setae, five strong setae anterior to spines and three additional setae down side, interiorly (latter may be easily overlooked; coxal endite terminally with eight spines and one strong seta,

FIGURE 5. Megalopal sensory and feeding appendages of *Pachycheles monilifer* (Dana); A, Antennule; detail of third peduncular segment on right; B, Antenna; C, Mandible; D, Maxillule; E, Maxilla; F, Maxilliped 1; G, Maxilliped 2; g, spine position on penultimate segment; H, Maxilliped 3; h, spine position on last three segments. Not all aesthetascs nor elongate setae are completely figured. Scale lines equal 0.3 mm.

on either side of which are six setae plus eight additionally adjacent to these; other setae lower down as illustrated. Endite prolonged into thin lobe fringed with fine hair and with two long setae basally.

Maxilla: (Fig. 5, E). Endites so heavily crowded with setae that numbers and position difficult to ascertain, but approximately as follows: basal endite, distal lobe, 36 or more terminally, proximal lobe, about 20; coxal endite distal lobe, 11 terminally and subterminally, plus eight or nine down the side, proximal lobe with 13 spines terminally, four behind these, plus 23 strong setae in ring around lobe; endopodite indistinctly two-segmented, probably only one segment, with six (less often four) long setae as illustrated; scaphognathite with about 60 to 72 setae around outer margin; other shorter setae and spinules on appendage endites as illustrated.

Maxilliped 1: (Fig. 5, F). Exopodite distinctly segmented at base, endopodite indistinctly so, setae on both as illustrated; protopodite divided into two lobes, setae on anterior lobe about 37, plus two posteriorly, and ten additional shorter setae behind and subterminally; on posterior lobe two rows, 10 terminally and seven subterminally, plus others as illustrated.

Maxilliped 2: (Fig. 5, G, g). Exopodite two-segmented, endopodite four-segmented, setae as illustrated. Those on terminal segments of endopodite crowded and much elongate, about 18–20; three additional large spines on penultimate segment as illustrated (detail).

Maxilliped 3: (Fig. 5, H, h). Coxopodite and basipodite as illustrated, extremely setose, with spine on former; exopodite two-segmented, four terminal setae plus others as illustrated; endopodite five-segmented, ischium, merus and carpus with lateral edges developed into dentate lamellae; a spine interiorly on ischium; remaining segments with numerous long setae in approximate numbers as follows: merus, 16; carpus; 16 propodus, 10 exteriorly, 13 interiorly; dactylus, 10 exteriorly, 7 interiorly. Dagger-like spines on last three segments as illustrated in detail (Fig. 5, h).

Pereiopods: (Fig. 6, A, B). All walking legs setose, with elongate spines ventrally on propodus and dactyl as illustrated. Pereiopod 5 chelate, with six long scythe-like setae laterally and ventrally, and others as illustrated. Surfaces of chelipeds, and walkings legs to a lesser extent, with distinct granulate rugae transversely in longitudinal rows; several small setae project from each ruga on chela, but not walking legs. Rugae are miniature version of rounded granules that adults exhibit. Outer margin of hand and fingers, dorsally and ventrally sculptured into single, bifid, or occasionally trifid, spinules. Anterior margin of carpus of chelipeds developed into four large, serrate, spine-like teeth.

Pleopods: (Fig. 6, C, D). Four pairs, simple biramous processes. Setae number inconsistent in the same specimen, but usually appearing as 13 + 1, 13 + 2, 14 + 2, 12 + 2, on exopodite and endopodite, respectively, progressing toward telson. Endopodites also with 4–5 hooks which function as *appendix interna.*

Tail Fan: (Fig. 6, E). Telson with eight or nine elongate marginal setae on either side of midline, plus smaller setae interspersed between these, number inconsistent in same specimen. Uropodites with setae on exopodites, 15–16, endopodites, 10–12, also inconsistent in same specimen. Ventral surface of telson with four, long distinct setae adjacent to cloaca, plus additional pairs dorsally and ventrally on midline, and elsewhere, as illustrated.

FIGURE 6. Megalopal locomotory appendages and tail fan of *Pachycheles monilifer* (Dana); A, Pereiopod 1; B, Pereiopod 5; C, Pleopod 1; D, Pleopod 4; E, Tail fan (dorsal view). Scale line equals 0.3 mm.

Color: Carapace a deep transparent blue throughout, chelipeds and pereiopods more transparent but of same blue color; entire megalopa peppered overall with numerous scattered red chromatophores, most prevalent as follows: on manus of cheliped forming a distinct red band; scattered dorsally on carpus of same, less so ventrally; walking legs banded with red anteriorly and posteriorly; additional scattered red chromatophores on epimera, and between walking legs 1 and 2 ventrally; on posterior margin of abdominal somites in interrupted line; dorsally on surface of telson in three large expanded groups; in addition, numerous white spidery or "snowflake" chromatophores on frontal region; eyes dark brown.

For comparative purposes the data on zoeal and megalopal stages in other species of *Pachycheles* are still quite sketchy, and even where complete development is known many inconsistencies appear in the same species (see *e.g.*, Table I and Discussion below). However, a provisional synopsis of zoeal features using the known data that seem most reliable may be of aid in identifying at least some of the porcellanid larvae in the plankton to the genus *Pachycheles*.

SYNOPSIS OF LARVAL CHARACTERS IN THE GENUS *PACHYCHELES*

Carapace

Rostral spine elongate in both zoeal stages, generally straight, not upswept, heavily spinose overall or armed only laterally and ventrally in some; lower mar-

gin of carapace serrate, dentate, with small curved hooks, on entire; postero-lateral margins may have distinct spinule.

Abdomen

Postero-dorsal margin of abdominal somites three through five with or without row of small teeth; postero-lateral spines present at least on somites four and five; pleopods on somites 2, 3, 4, 5, in stage II.*

Antenna

Stage I exopodite longer than endopodite; three to four spines distally in a row. Stage II exopodite shorter than endopodite, armature reduced or lacking.

Mandible

Without palp in stage I; palp usually present in stage II.*

Maxillule

Endopodite with four setae both stages.

Maxilla

Endopodite with nine setae both stages, usually placed 4, 3, 2.

Maxillipeds

Setae on terminal endopodal segments different depending on species; maxilliped 1 penultimate segment usually with 2 medial, 3–4 distal setae;* maxilliped 2 formulae usually 2, 2, 1 + 2, 5 + 1 in stage I, with one additional dorsal seta (= I) added to segments 1–3, both maxillipeds, in stage II;* (dorsal seta on segment 1 may be lacking in some species).

Telson

First two elongate plumose setae armed distally with hook-like spinules, remainder not armed in most species; fifth pair plumose setae on central prominence in stage I, a median spine added here in stage II.*

These features marked thus * also occur in larvae of *Petrolisthes* and *Megalobrachium* to some extent. Such "suprageneric" characters have been used to classify larvae of these two genera along with *Pachycheles* in the *Petrolisthes*-group of larvae based on an original grouping by Lebour (1943). Other larvae differing in some or all of these features are currently assigned to either the *Porcellana*-group or the *Petrolishthes platymerus*-group (see Gore, 1971, 1972b, for a more complete discussion).

Although even less data are available for megalopal stages in the genus some features appear to be consistent. The megalopa, in general, seems to resemble the adult to some degree, the margin of the frontal region is often serrate or with distinct setae dorsally, spinules may be present along the epibranchial margin of

the carapace, the third antennular peduncle segment may have two groups of elongate setae dorsally and ventrally, the lamellar plates of the ischium, merus and carpus of maxilliped 3 are often dentate, and two pairs of elongate setae may appear on the ventral surface of the telson adjacent to the cloaca.

Discussion

The zoeal stages of *Pachycheles monilifer* may be identified in the plankton by several features. Most notable is the color of the live zoeae which appear even to the unaided eye to be banded with orange on the abdomen, and diffused with orange on the rostral and posterior carapace spines. Other features in the first zoeal stage include the distinctly spinulose lower margin of the carapace, the large recurved spinules on the posterior carapace spines, the small teeth dorsally on the posterior margin of abdominal somites three to five, the three small spines in a row on the antennal exopodite and the large hook-like spinules on the distal tips of plumose telson setae 1 and 2.

In the second stage *P. monilifer* possesses carapace spinulation only on the postero-lateral margin, but retains the enlarged spinules proximally on the posterior carapace spines, the small teeth on the postero-dorsal margin of the abdomen and the hook-like spines on the distal tips of telson setae 1 and 2. Three fine hairs replace the row of spines on the antennal exopodite. In addition, second stage *P. monilifer* possesses a median spine on the telson which places it in Lebour's (1943) category of the *Petrolisthes*-group of larvae, the group to which other known members of the genus belong (see Knight, 1966; Boschi, Scelzo and Goldstein, 1967, MacMillan, 1972).

The megalopal stage of *P. monilifer* has a noticeably spinulose frontal margin, dentate epibranchial angles, and heavily spined chelipeds covered dorsally with distinct longitudinal rows of rugae or enlarged granules. Other easily observed features include the dentate lamellar segments of maxilliped 3, the numerous short hairs on the frontal region, the elongate setae groups on the dorsal and ventral margins of the terminal segment of the antennule, and the two pairs of elongate setae ventrally on the telson adjacent to the cloaca.

In the megalopae the sidewalls of the carapace are not yet divided into the additional plates which characterize adults of the genus. However, sutures appear postero-laterally in this region and division of the epimera probably occurs during early crab stages. The telson also is not yet divided into five plates, nor is there any way to distinguish male pleopods at this stage, much less to be able to forecast their presence or absence at sexual maturity. Except for these features, the megalopae resemble the adult in many respects, most notably in the ornamentation of the dorsal and anterior surfaces of the chelipeds.

The blue color of the carapace and chelipeds and the numerous scattered red chromatophores, especially those which form bands of red on the manus and the walking legs, may also aid in identification of this species at this stage of development.

All of these colors are lost upon molt to first crab stage whereupon the animal assumes a mottled greenish-brown and white color which becomes more intense and less muddy in later crab stages as the animal progresses through the juvenile state.

Pachycheles haigae is the only other species of the genus in the western Atlantic for which the complete development is known (Boschi, Scelzo and Goldstein, 1967). Although *P. haigae* has not been recorded north of Pernambuco, Brazil (7°–10° S; in Boschi, 1963; also Coelho, 1963), *P. monilifer,* on the other hand, has been reported as far south as the state of Sao Paulo, Brazil (about 25° S; in Haig, 1966a). The larvae of these two species, therefore, overlap between these two areas and might possibly be confused. However, the study by Boschi *et al.* (1967) is quite thorough and by referring to that work the larvae of the two species should be easily distinguished. Briefly, *P. haigae* differs from *P. monilifer* in having the rostral spine unarmed dorsally, the posterior margin of the carapace unarmed except for a single spinule, in having four (not three) spines in a row on the antennal exopodite in stage I and being unarmed in stage II, possessing a different number (*i.e.* formula) of setae on both maxillipeds, and, most exceptionally, in lacking a palp on the mandible in stage II. Both zoeal stages apparently lack the small teeth on the postero-dorsal margin of the abdominal somites which are present in *P. monilifer.*

The megalopal stage of *P. haigae* may be distinguished by its rosy-red color, by lack of spination on the frontal and epibranchial regions (according to the illustrations examined), by the reduced carpal spines on the cheliped, and by the presence of only five elongate dorsal and lateral setae on the third or terminal segment of the antennular peduncle.

I have also a very limited series of laboratory-cultured first zoeae of *Pachycheles serratus,* another western Atlantic species. In these zoeae the following differences appear: the entire lower margin of the carapace is armed with small, rounded, anteriorly-directed hook-like spinules, the antennal exopodite has two or three very small, hair-like spines, and the setae number and position on the first two maxillipeds is 3, 3, 2 + 4, 10 + I, and 2, 2, 1 + 2, 5 + I, respectively. The first zoea of *P. serratus,* unlike those of *P. monilifer,* has only a few minute teeth on the postero-dorsal margin of the abdominal somites. The first two elongate plumose setae on the telson, however, do possess distinct hook-like spinules distally.

In the eastern Pacific Ocean, larvae are known for *Pachycheles rudis* and *P. pubescens,* both of which are not known to occur farther south than the Baja California peninsula. Comparison of *P. monilifer* with *P. rudis* and *P. pubescens* shows that the larvae of all three are quite similar (Table I). In the first zoeal stage of these species the chief differences appear in the length ratio of the antennal endopodite and exopodite, in the spinulation on the postero-dorsal margins of the abdominal somites, and whether the lower margin of the carapace is armed. The only difference in maxilliped setation which does not appear to show variation is that of the ventral setae on the second endopodal segment (3 in *monilifer* and *pubescens,* 2 in *rudis*). This last feature must therefore be used with care at the species level.

In stage II the species differ in the presence or absence of a single long seta on the antennular protopodite next to the junction with the endopodite, in the armature of the antennal exopodite, the number of setae on the exopodite of maxilliped three, and in the abdominal-somite and carapace-margin features mentioned previously. *P. rudis* lacks a dorsal seta on the first endopodal segment of both maxilliped 1 and 2, and this basipodal and endopodal ventral setation may allow

the species to be distinguished from *P. monilifer* and *P. pubescens*. Apparently, variation in setae formulae does not occur as often in stage II as in stage I. The number of setae around the margin of the scaphognathite might also prove to be a valuable character at the species level.

At the megalopal stage little difficulty should be encountered in live material since, as far as is known, only *P. monilifer* is colored blue with scattered red chromatophores. In preserved specimens the armature of the anterior margin of the carpus of the cheliped should be distinctive (4 spines in *monilifer*, 2 in *pubescens*, 1 in *rudis*).

An examination of Table I shows that several features are recurrent and may thus be indicative at the generic level. These include the presence of spines or spinules on the antennal exopodites in stage I, plus four setae on the endopodite of the maxillule, and the hook-like spinules on the distal tips of the first two elongate plumose telson setae in both zoeal stages (except in *P. natalensis*). The setal formula of the maxillary endopodite may also have value since the number is usually 9 setae, and the positioning appears to be 4, 2, 3, in most cases, based on either descriptive text or good illustrations. This last features must also be used with caution since the determination as to whether setae are terminal or subterminal is, at times, quite subjective. In the known species of *Petrolisthes*, for example, some also have 9 setae on the maxillary endopodite, but these are placed 3, 3, 3; thus, this feature is of limited value at present when used by itself at the generic level. Other features of somewhat limited value are the previously noted spinules on the postero-dorsal margins of the abdominal somites and the armature of the lower carapace margin. Both features occur inconsistently in some species or are lacking entirely. Both features, because of their small size, required higher objective magnification (20× – 40×) to be seen, hence they might have been inadvertently overlooked in those species in which they are described as absent.

MacMillan (1972) noted that both *P. rudis* and *P. pubescens* lacked setules on the dorsal margins of the maxillipedal endopodites, and suggested this as a possible generic character for *Pachycheles* larvae. However, setules are present in both *P. monilifer* and *P. serratus* and are apparently indicated in *P. natalensis* (see Sankolli, 1967, page 748, Fig. 2,g). Thus, this feature becomes less useful as a generic character, especially in larvae from two of the three known Atlantic species, although it presently may still be used to distinguish these from the two known eastern Pacific species.

It is entirely possible, of course, that some of the features noted in the discussion above and in the earlier synopsis may ultimately prove to be unreliable or too inconsistent to be safely used at the generic level. This would not be unexpected in such a large and widespread genus as *Pachycheles*. Nor would it be surprising to find some of the above noted features also occurring in larvae of the closely related genus *Neopisosoma*. Future studies, carefully done, may not only clarify such relationships but provide additional or more stable criteria for determining planktonic porcellanid larvae at the generic level.

I thank Dr. Mary E. Rice, National Museum of Natural History, and Mr. Douglas S. Putnam, Harbor Branch Foundation Laboratory, Ft. Pierce, Florida

(HBFL) for providing one of the ovigerous specimens used in this study. Mr. R. Grant Gilmore (HBFL) helped me collect the other specimens and aided in the laboratory in many ways. I also extend my thanks to Dr. Anthony J. Provenzano, Jr., Ocean Protein Corporation, Dania, Florida, for criticism and advice regarding the manuscript. The Harbor Branch Foundation Laboratory provided facilities and equipment for completion of this study.

Summary

The complete larval development from hatching through megalopal stage is described and illustrated for *Pachycheles monilifer*, a shallow water porcellanid crab. The development at room temperature (27.8° C) under laboratory conditions consisted of a prezoeal stage of approximately one hour duration, two zoeal stages of approximately five and six days duration, respectively, and a megalopal stage of about eight days duration. The entire larval/postlarval portion of the life cycle is completed under the conditions described herein in approximately three weeks.

The zoeal and megalopal stages of *P. monilifer* were compared with larvae known from two other western Atlantic species, and two species each from the eastern Pacific and Indo-Pacific oceans. As might be expected, larvae of the genus are quite similar in many respects, and difficulty may be encountered in separating them at the specific level. However, certain morphological features are recurrent in the zoeal stages and may be indicative at the generic level; among these are the presence of three spines on the antennal exopodite, four setae on the maxilliulary endopodite, and the hook-like spinules on the first two elongate plumose setae of the telson. A provisional synopsis is provided utilizing the most salient features occurring in all known *Pachycheles* larvae as an aid in recognizing such larvae, at least at the generic level, in the plankton.

LITERATURE CITED

Boone, Lee, 1932. A collection of anomuran and macruran crustacea from the Bay of Panama and the fresh waters of the Canal Zone. *Bull. Amer. Mus. Natur. Hist.*, **63**: 137–189.

Boschi, E. E., 1963. Sobre dos especies de *Pachycheles* de la Argentina. *Neotropica*, **9**: 31–37.

Boschi, E., M. A. Scelzo and B. Goldstein, 1967. Desarrollo larval de dos especies de Crustáceos Decápodos en el laboratorio. *Pachycheles haigae* Rodrigues da Costa (Porcellanidae) y *Chasmagnathus granulata* Dana (Grapsidae). *Bol. Inst. Biol. Mar. Nac. Buenos Aires*, **12**: 1–46.

Coelho, P. A., 1963. Lista dos Porcellanidae (Crustácea, Decápoda, Anomura) do littoral de Pernambuco e dos estados vizinhos. *Trab-s. Inst. Oceanogr. Univ. Recife*, **5/6**: 51–68.

Dana, J. D., 1852. Crustacea. Part 1 in *United States Exploring Expedition during the years 1838, 1839, 1840, 1841, 1842, under the command of Charles Wilkes, U. S. N.*, Volume **13**. *Philadelphia, Pennsylvania*, 685 pp.

Dana, J. D., 1955. Crustacea. Atlas in *United States Exploring Expedition during the years 1838, 1839, 1840, 1841, 1842, under the command of Charles Wilkes, U. S. N.*, Volume **14**. Philadelphia, Pennsylvania, 27 pp.

Gonor, Sue Lewayne, 1970. The larval histories of four porcellanid anomurans (Crustacea, Decapoda) from Oregon. *Masters thesis, Oregon State University*, 106 pp.

Gore, R. H., 1970. *Petrolisthes armatus:* A redescription of larval development under laboratory conditions (Decapoda, Porcellanidae). *Crustaceana*, **18**: 75–89.

Gore, R. H., 1971. *Megalobrachium poeyi* (Crustacea, Decapoda, Porcellanidae): Comparison between larval development in Atlantic and Pacific specimens reared in the laboratory. *Pacif. Sci.*, **25**: 404–425.

GORE, R. H., 1972a. *Petrolisthes armatus* (Gibbes, 1850): The development under laboratory conditions of larvae from a Pacific specimen. (Decapoda; Porcellanidae). *Crustaceana,* **22**: 67–83.

GORE, R. H., 1972b. *Petrolisthes platymerus:* The development of larvae in laboratory culture (Crustacea: Decapoda; Porcellanidae). *Bull. Mar. Sci.,* **22**: 336–354.

GORE, R. H., AND L. G. ABELE, 1973. Three new species of porcellanid crabs (Crustacea, Anomura) from the Bay of Panama and adjacent Caribbean waters. *Bull. Mar. Sci.,* **23**: in press.

HAIG, JANET, 1956. The Galatheidea (Crustacea Anomura) of the Allan Hancock Atlantic Expedition with a review of the Porcellanidae of the western North Atlantic. *Rep. Allan Hancock Atlan. Exped.,* **8**: 1–45.

HAIG, JANET, 1960. The Porcellanidae (Crustacea Anomura) of the Eastern Pacific. *Rep. Allan Hancock Pacif. Exped.,* **24**: 1–440.

HAIG, JANET, 1966a. Porcellanid Crabs (Crustacea Anomura). *Result Scient. Comp. Calypso,* **7**: 351–358.

HAIG, JANET, 1966b. A review of the Indo-west Pacific species of genus *Pachycheles* (Porcellanidae, Anomura). *Proc. Symp. Crustacea, Mar. Biol. Ass. India,* **1**: 285–294.

KNIGHT, MARGARET D., 1966. The larval development of *Polyonyx quadriungulatus* Glassell and *Pachycheles rudis* Stimpson (Decapoda, Porcellanidae) cultured in the laboratory. *Crustaceana,* **10**: 75–97.

KURATA, H., 1964. Larvae of decapod crustacea of Hokkaido. 7. Porcellanidae (Anomura). *Bull. Hokkaido Reg. Fish. Res. Lab.,* **29**: 66–70.

LEBOUR, MARIE V., 1943. The larva of the genus *Porcellana* (Crustacea, Decapoda) and related forms. *J. Mar. Biol. Ass. U. K.,* **25**: 721–737.

MACMILLAN, F. E., 1972. The larval development of northern California Porcellanidae (Decapoda, Anomura). 1. *Pachycheles pubescens* Holmes in comparison to *Pachycheles rudis* Stimpson. *Biol. Bull.,* **142**: 57–70.

SANKOLLI, K. N., 1967. Studies on larval development in Anomura. (Crustacea, Decapoda). I. *Proc. Symp. Crustacea, Mar. Biol. Ass. India,* **2**: 744–776.